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# BIOLOGICAL BULLETIN

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## THE PROGRESSIVE ODOR OF ANTS.

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### I. STATEMENT OF HYPOTHESES BASED ON RECENT AND FORMER EXPERIMENTS.

1. *The Specific Odor.*—The mother-ant transmits to her offspring the distinctive odor which is identical for ants of all ages and of both sexes within the species. This odor is appreciated among ants by organs near the proximal end of the funicle.<sup>1</sup>

2. *Progressive Odor.*—Female ants, including queens and workers, have, besides their specific odor, an odor which may be termed progressive. Queens of different lineage have different progressive odors. In a queen this odor is either unchanging or changes very slowly, and it is similar to that of her newly-hatched female offspring.

a. As worker-ants advance in age their progressive odor intensifies or changes to such a degree that they may be said to attain a new odor every two or three months. This progressive odor is appreciated among ants by organs in the penultimate joint of the funicle.<sup>2</sup>

b. Male ants have no progressive odor unless it be superficially incurred through association with workers; but the male carries latent in his spermatozoa the progressive odor of his mother. In other words the progressive odor is always recessive in the male ant.

c. The progressive odor of each new generation of females is

<sup>1</sup> "Artificial Mixed Nests of Ants," A. M. Fielde, BIOLOGICAL BULLETIN, Vol. V., No. 6, November, 1903, p. 320.

<sup>2</sup> "Farther Study of an Ant," A. M. Fielde, *Proceedings of the Academy of Natural Sciences*, November, 1901, p. 531.

determined by the odor of the mother latent in her egg, and the odor of the father's mother latent in the spermatozoön. The progressive odor therefore changes in each generation of females.

d. The progressive odor manifest in female ants is the cause of the separation of ants of the same species into hostile colonies, and is of great advantage to the ants in their individual and their communal life.

3. *The Incurred Odor.*—An ant may incur from its associates an odor which is not inherent in itself, and which may be removed by washing. It may be transferred from ant to ant through air or through water. It arises from the substances that give the specific odor and the progressive odor and that create the nest-aura.

## II. RECENT EXPERIMENTS WITH THE PROGENY OF A SINGLE QUEEN, *COMPONOTUS PENNSYLVANICUS*.

In 1901 I found that the odor of working-ants of *Stenamma fulvum piceum* changes with their age,<sup>1</sup> forty days being the minimum of time in which there occurs a change so great as to effect the behavior of ants of the same colony toward one another at their first meeting.

In 1902 my further experiments indicated that a cause<sup>2</sup> for the hostility of one colony toward another of the same species and variety is a difference in odor coincident with difference in the age of the colonies.

In 1904 my observations on several species of ants,<sup>3</sup> representing three subfamilies, gave further evidence of their change of odor with advance of age, and indicated that the odor of the queen is unchanging, or that her odor changes much more slowly than does that of the workers.

I have now had under observation for more than two years a colony of *Camponotus pennsylvanicus*, in which the assertion of a

<sup>1</sup> "A Study of an Ant," *Proceedings of the Academy of Natural Sciences of Philadelphia*, July, 1901, p. 449.

<sup>2</sup> "Notes on an Ant," *Proceedings of the Academy of Natural Sciences of Philadelphia*, September, 1902, p. 609; "Cause of Feud Between Ants of the Same Species," *BIOLOGICAL BULLETIN*, Vol. V., No. 6, November, 1903, p. 328.

<sup>3</sup> "Power of Recognition Among Ants," *BIOLOGICAL BULLETIN*, Vol. VII., No. 5, October, 1904, p. 244.

progressive odor in the workers is definite and indisputable, the five successive broods included in the experiment being the issue of one queen.

*The N Queen.*—This queen was captured on Nonamesset Island, July 28, 1903. She was then deãlated and was probably the mother of the hundred workers seen in her wild nest, and also of the ants that afterwards hatched from the many cocoons brought with her to the laboratory. She remained under my care and, unless another is indicated, she is the queen referred to in the herein recorded experiments.

*The N1 Group of Workers.*—Some of the captured workers were transferred to Dr. Irving A. Field, and they remained segregated in his care, usually at Harvard University, until the time of the experiment in which they appear. As no other than male offspring had appeared in this group during the two years of its separation from the queen mother, the workers composing it in August, 1905, were certainly acquainted with the queen previous to her capture in July, 1903. Of the age of these workers of course nothing more was known than that it exceeded two years.

On August 6, 1905, I introduced into this nest,<sup>1</sup> where there were six major and five minor workers and about thirty larvæ from their own eggs, the queen-mother from whom these eleven workers had been separated for two years. The queen showed instant hostility, seized a major worker by one of its mandibles, braced herself on the sponge and held her prisoner there during the ensuing seven hours. All the other workers, sometimes six at a time, examined the queen meanwhile. They patted her with their antennæ, nabbed her gently, and licked her back and legs. Two of them, touching her body with their antennæ, appeared to dance for joy, shuffling their feet with great rapidity during several consecutive minutes. The queen then began to drag the worker that she had seized, and upon my releasing the latter, took a position near the larvæ-pile, as if to claim her incipient grandsons as her exclusive property, opening her mandibles at every worker who approached. Then followed a most curious and pro-

<sup>1</sup> All the artificial nests referred to in this paper were of the Fiedle pattern. See "Portable Ant-Nests," BIOLOGICAL BULLETIN, Vol. VII., No. 4, September, 1904.

longed effort on the part of the workers to placate the queen-mother. They surrounded her at all times, offering her regurgitated food. Whichever way she turned, there stood a humble servant with a proffered mouthful of pabulum. As many as seven workers simultaneously offered nourishment to her. Every worker of the eleven seemed bent upon wooing and winning her, and she was not for a moment left without attention. These efforts were unceasingly continued, and were meeting with a fair degree of success, when I removed the queen on the following morning.

This experiment showed that the workers all recognized the odor of their queen after two years of separation from it, and that the segregated workers had during the same interval acquired an odor unfamiliar to the queen, who had meanwhile met none of her daughters who were over fifteen months old. It also showed that major workers, having in this species nearly the same form and sometimes nearly the same bulk as has the queen, are like minor workers in having a progressive odor.

On August 7 I introduced into this N1 group a marked major and a marked minor worker, daughters of the N queen, but many months younger than any of the ants in this group. The visitors were received with signs of curiosity, but with perfect amiability, though no younger sisters had been encountered within two years by these N1 ants. The odor of the younger sisters was perfectly recognized by the eleven residents, and I removed the former.

I then introduced a young winged queen of the same species, *Camponotus pennsylvanicus*, but of an alien colony. The resident ants attacked her instantly and with exceeding virulence. In an instant she lost an antenna, one worker was pulling out her remaining antenna, and three others were dragging her by her legs. The scrimmage was fierce, and before I removed the intruder four of the residents had received injuries that resulted in their deaths. The residents had given to the alien queen a reception strongly contrasted with that accorded to their own queen-mother; while the havoc wrought by the alien queen indicated that, if unable to escape from the nest, she might have destroyed all the workers and have remained a fostering mother to their larvæ.

*The N<sub>2</sub> group.*—During the first week in August, 1903, the queen deposited about a hundred eggs, and from these were reared five minor workers, denoted here as the N<sub>2</sub> ants. These workers hatched between April 24 and May 10, 1904, and were therefore some fifteen months old at the time of the experiment here recorded. These workers had never met other ants than those of their own segregated group, and were therefore unacquainted with the odor of ants in any wise unlike themselves. They had never lived with the queen, had laid no eggs, and had the care of no young. On July 16, 1905, I put these ants into a new and very small nest where I had isolated the queen-mother without young. The five workers were wholly at ease with the queen, and hastened to evince their devotion in ant fashion; but the queen opened her jaws whenever they approached her, and was somewhat querulous in her behavior during the ensuing two days. The queen had lived during the previous five months with daughters, all minor ants, less than five months old, and her behavior indicated a difference in the odor of her younger and her older daughters. Her memory was manifestly less tenacious than that of the workers, who, on their part recognized in their queen the odor that had been their own in their infancy, fourteen months earlier.

*The N<sub>3</sub> group.*—This group consisted of two major workers hatched in July, 1904, and four of their younger sisters, minor workers, over five months and less than a year old, all the issue of the N queen. The two majors were acquainted with sisters older than themselves, while the minors knew no sister older than these two majors. The members of this group had all lived with the queen, and had been separated from her and living in segregation since February 14, 1905. They had deposited no eggs, and they had the care of a few introduced larvæ. On July 18, 1905, I introduced into this group a sister nine months older than the oldest in the group. The majors, who had had acquaintance with sisters much older than themselves, did not attack the newcomer at all, while every one of the minors, never having met a sister so old as was the visitor, attacked, dragged and finally killed her.

It appeared that the behavior of the two major workers was

dictated by memory, while that of the four minor workers was an effect of hostility created by the presentation of an unfamiliar odor. The major workers were either wanting in compassion, or else they lacked means of communicating with their younger sisters, for although they were each double the size of any minor ant in the group, they did not interfere in behalf of the victim.

*The N<sub>4</sub> Group.* — The queen was transferred without eggs or young to a new nest on July 14, 1904. She laid no eggs thereafter until December, 1904, and from the eggs then deposited the five minor workers constituting the N<sub>4</sub> group were hatched between February 19 and March 23, 1905. These workers were therefore four or five months old at the time of the experiment. On July 16, 1905, I removed the queen from the nest, leaving the five workers in charge of twenty larvæ, the issue of the queen's December eggs. Into this group of five minors, who had never met older sisters, I introduced one of the majors from group N<sub>3</sub>, now just a year old, and twice or thrice the bulk of any of the five residents. The introduced ant was instantly and violently attacked by three residents. This attack indicates that the major, like the minor ants, like in shape and size as they are to the queen, change their odor with advance in age, as do minor workers.

Having removed this visitor, I introduced a marked large minor worker, fourteen months older than the residents, a sister of theirs, hatched from eggs deposited by the queen in August, 1903. This visitor was likewise violently attacked, every one of the five residents manifesting hostility to her, and the next day I found her mangled body on their rubbish pile.

*The N<sub>5</sub> Group.* — This group consisted of two minor workers, the issue of the queen's December eggs, sequestered in their cocoons and hatched on September 8, 1905. They were at once placed in segregation in a new nest, with a few larvæ and cocoons from their mother's eggs. Ten days later these ants drove away from their pile of young any member of the N<sub>4</sub> group of sisters six months older than themselves.

In these experiments it appears that it is the age of the workers, not the age of the queen at the time when she deposits the eggs from which the workers issue, that determines at any date

their progressive odor. All the ants engaged in this last mentioned experiment were certainly the issue of the eggs laid by the queen early in December, 1904. That there is similar progress in odor among ants of the same age and species is indicated by an immediate and amicable association of ants that are reunited after a period of separation so long as two years.<sup>1</sup>

Whether two mutually hostile groups could be created from among the worker-progeny of a single queen would depend on power of memory in the older workers. By segregating from the pupa-stage the broods of different summers, it would be found that the younger sisters would always be hostile to the older sisters, because the older sisters would present an unfamiliar odor to the younger. The hostility of the older sisters toward the younger would be nullified by their memory of the odors by which they had themselves been characterized at earlier periods in their own lives. If the younger sisters bore an odor which the older sisters, through the lapse of many years, should have forgotten, then the hostility would become mutual. It is certain that worker-ants can remember for years an odor with which they have once become familiar, and it is probable that they remember such odors as long as they live.

When ants of different groups meet amicably, either the members of these groups have the same odor, or else they have at some time in their lives been familiar with ants bearing the presented odor. If one group recognizes a familiar odor, while the other group discerns a strange odor, then those finding themselves among strangers will try to escape, or will make attack. There is no love at first sight between ants of different odors.

### III. THE ODOR AND THE SENSE OF SMELL IN MALE ANTS.

Male ants apparently bear a specific odor, beside the odor that may be incurred during their residence with nurses in the home nest. I have introduced males of different species into the nests of *Stenamma fulvum*, *Cremastogaster lineolata*, *Myrmica rubra*, *Formica sanguinea*, *Formica Schaufussi*, *Camponotus pennsylv-*

<sup>1</sup> "A Cause of Feud Between Ants of the Same Species Living in Different Communities," A. M. Fields, BIOLOGICAL BULLETIN, Vol. V., No. 6, November, 1903, p. 327.



*vanicus*, *Camponotus pictus*, *Camponotus americanus*, *Lasius latipes*, and *Lasius umbratus*, and all these males have invariably been killed within a day or two. If hybridization is to be effected among ants it will be necessary to cause the males and females to become acquainted with one another within a few hours after hatching. When hatched in the same nest, males of *Stenamma fulvum* pursue queens of *Cremastogaster lineolata* with the same ardor that they show in pursuing queens of their own species. In my mixed nests the failure of individuals of these two genera to mate was manifestly due to physical and not to psychic incompatibility.

In the summer of 1905 I had material in my stock of ants for experiments giving evidence that the male ant has at hatching the specific odor of his virgin worker-mother. My E mixed nest consisted of workers of *Camponotus pictus*, *Formica neogates*, *Formica subsericea*, and *Stenamma fulvum*, all hatched during the last week of July, 1904, and kept in the same nest until the first day of January, 1905, when the *Stenammias* were segregated apart. They remained in segregation until August 22, 1905, when I put into their small nest, where there were ten workers and a few eggs, a fine male *Camponotus pictus*, the offspring of a virgin worker-mother who had shared the nest of these *Stenammias* until she was five months old. This young male was received by the resident *Stenammias* with evident pleasure. They licked him, regurgitated food to him, and rode on his back. He continued to live happily with them for many days. He bore a familiar specific odor, although hatched among segregated workers of his species, eight months older than any that these *Stenammias* had known; and this familiar odor made him welcome. His fate was in strong contrast to that of some of his brothers or cousins introduced into another nest. At the time of these experiments I had also a nest, marked D, of eleven *Stenamma fulvum* workers, that had hatched in a mixed nest during the last half of August, 1903, and had lived for several months with *Camponotus pennsylvanicus*, and *Formica subsericea*, but had never met a *Camponotus pictus*. These eleven *Stenammias* had lived in segregation since July 17, 1904, and were destitute of young, when on August 22, 1905, I introduced into their nest

a newly hatched *Camponotus pictus* male, the offspring of a virgin worker, a brother or cousin of the one in the E nest above mentioned. These ants of the D nest at once began to harry him, and although he was eleven millimeters long and very sturdy, while none of the *Stenammæ* were more than five millimeters in length, they harried his life out within two days. Repetitions of this experiment gave similar results in every case.

The eggs from which these *Camponotus pictus* males were produced were deposited by their virgin worker-mothers in May, 1905, five months after the said mothers were separated from the *Stenammæ* that the said mothers had lived with during the first five months of their lives. It therefore appears that the male progeny of virgin workers have not the progressive odor which characterized their mothers. The males have, however, a specific odor, an odor recognized by the ants through certain joints of the antennæ, and this odor is doubtless the stimulus calling forth the exceeding care given by the workers to young males with whose specific odor they are familiar.

On August 26 I put into each nest, the E and the D nests above described, two males of *Stenamma fulvum*. These males, the first of their species ever encountered by these workers, were treated alike in the two nests. They were so eagerly grasped by several residents at once that it seemed as if they must lose their lives through the determined efforts of the workers to retain them. They were not left free for several hours; but so judicious were their virgin captors that no injury was done to the captives, and they lived in health and honor many days in these nests. In the E nest the *Camponotus pictus* male continued to be their associate.<sup>1</sup> In both the E and the D nests newly hatched

<sup>1</sup> A deâlated queen *Camponotus pictus* captured alone in the open on July 5, was kept in isolation till August 15, 1905, when she received amicably into her small artificial nest two young males of her species, the offspring of virgin worker ants. She licked them, regurgitated food to them, and during the several days that they remained under my observation, remained in close companionship with them. Later on this queen also received in amiable fashion the virgin mothers of these males, the worker-mothers having been kept by me in segregation during their whole lives. As this queen was captured near the spot in which the workers had their origin a year earlier, these ants may all have been of one colony. This queen killed young males of *Formica argentea* and *Stenamma fulvum* introduced into her nest.

*Stenamma* workers, from the same colony as were these males, were immediately killed.

Since the males avoid, or are indifferent to, ants of other species than their own, unless hatched among such species in artificial nests, it appears probable that they discern the specific odor of other ants. But they probably lack the sub-nose that perceives the progressive odor of workers. Male ants of various species placed under observation in one of my artificial nests, grouped themselves according to species, but did not quarrel with males of species unlike their own. I infer that the only inherent odor of males is that of their species; but that they are the medium through which the progressive odor of their female progenitors is transmitted to the egg that produces a female, the progressive odor being latent in the males and reappearing in their female descendants. Only the egg receiving a spermatozoon would produce a female, and this female would be endowed with her paternal grandmother's tendencies in progressive odor, the progressive odor thus manifesting itself only in the female line of descent. The fact that the worker progeny of a queen, sequestered from the pupa stage, will receive their queen-mother or the queen-mother's sister with equal pleasure, indicates similarity of odor in the product of the same queen's impregnated eggs.

I venture to predict that there will be found in female ants secretory glands or organs that are wanting or are rudimentary in the male, and that these organs are the producers of the progressive odor. There must be in both males and females secretory glands or organs producing the specific odor which is common to both sexes. These diverse organs might be identified through the possession of both sets by the female and of a single set in the male. It is also probable that the male lacks the glands that secrete the scent whereby the female lays down her individual path from the nest, and he may also lack the sub-nose which discerns this path-scent. The male seems to be unable to lay a path, and, in a change of domicile by the colony, he is carried bodily by the females to the new nest. It is through his appreciation of the specific odor and his lack of perception of the

progressive odor that the male is best fitted for his distinctive office in the ant world.

#### IV. THE PROGRESSIVE ODOR OF QUEEN ANTS.

The change in the inherent, transmissible, progressive odor in a line of queens is probably slow and cumulative, but that such a change occurs is evidenced by the behavior of any segregated group of *Stenamma fulvum* workers, a species in which the queens generally remain in the colony in which they are produced. When workers from such a colony are segregated from the pupa-stage upward, it becomes difficult to find, in the wild nest, any queen that these segregated workers will accept as their own. In this species, I have reared worker-offspring from queens that were sequestered from all males except those of their own colony,<sup>1</sup> and these workers willingly associated with their worker-cousins. That the change of odor is but slight in a single generation is also shown by the fact that the worker-daughters of a queen, after having been segregated from their pupa-stage upward, and with no criterion of odor save that of their own bodies, will affiliate with their queen-mother at a first meeting, though they always examine her with exceeding care before rendering complete homage.

The gradual change in odor, through the introduction of the male element, from generation to generation, may be crudely represented by the use of letters as symbols of the odor of queens of the same species and variety.

The Roman numerals at the left denote successive generations of mated queens.

The letter *a* is used as a symbol of the odor characterizing two sister queens; the other letters as symbols of the odor inherited from the paternal grandmother.

I. <i>a</i> ,	I. <i>a</i> ,
II. <i>a</i> + <i>b</i> ,	II. <i>a</i> + <i>l</i> ,
III. <i>a</i> + <i>b</i> + <i>c</i> ,	III. <i>a</i> + <i>l</i> + <i>m</i> ,
IV. <i>a</i> + <i>b</i> + <i>c</i> + <i>d</i> ,	IV. <i>a</i> + <i>l</i> + <i>m</i> + <i>n</i> ,
V. <i>a</i> + <i>b</i> + <i>c</i> + <i>d</i> + <i>e</i> ,	V. <i>a</i> + <i>l</i> + <i>m</i> + <i>n</i> + <i>o</i> ,
etc.	etc.

<sup>1</sup> "Notes on an Ant," *Proceedings of the Academy of Natural Sciences of Philadelphia*, December, 1902, p. 605.

The female descendants of sister queens would thus become more unlike in odor with every generation.

An odor providing the means of recognizing a maternal ancestor, or another descendant of that ancestor, may be dominant through more than one generation of females.

The fact that worker ants who have never met any queen will as joyfully associate with their queen-mother's sister as with their own mother, indicates that sister-queens have the same odor after mating that they had before mating, and that the first divergence in odor becomes apparent to the ants only in the offspring of sister-queens that mated with males capable of imparting unlike odors to their respective progeny. The worker ants, having attained the distinctive progressive odor characterizing their mothers' worker-offspring for the current year, may produce males who will each impart to his progeny the distinctive odor borne by all the female issue of the queen with whom he mates. Each generation in the line of queens would then depart farther from the odor of the queen ancestor, and we should find, as we do, colonies in which all the female inhabitants are inimical to all the female inhabitants of another colony. There would also be produced, as in colonies of *Stenamma fulvum*, where queens mate within the nest and remain to increase its population, the phenomenon of callows that, if segregated from the pupa-stage, refuse to affiliate with queens from the nest in which were deposited the eggs from which these callows issued.

During several years I have been interested in ascertaining whether adult, queenless workers would willingly accept a queen who was indisputably of another colony of their own species, and among many experiments I have never seen such an acceptance. If forced into association, escape of either party being made impossible, the workers may after a longer or shorter interval live peaceably with the alien queen, as they also may do with alien workers. But such forced alliances do not result in normal prosperity, even when a whole year is allowed for the cementing of friendship. So exacting are the ants concerning adherence to their standard of odor that they prefer a queenless state to the presence of an unknown ant-odor. Observations made by me in the summer of 1905 accord with my earlier ones. Eleven

workers of *Stenamma fulvum piceum* had been inmates of one of my mixed nests, with *Camponotus pennsylvanicus* and *Formica subsericea*, all hatched between August 14 and September 3, 1903. The *Stenammæ* had been removed from the mixed nest, and kept in segregation since June 23, 1904, and had never met a queen. On August 13, 1905, I introduced into this nest a young, winged queen of the same variety as these workers, on the twenty-fourth day after I had isolated her to ensure her freedom from incurred odor. The queen fled from the group of workers and constantly tried to escape. She was attacked whenever I forced her into the group of workers, and was caught and killed by them on the ninth day of her sojourn. A dealated queen introduced later, from the wild colony to which these workers originally belonged, was also killed by them.

Since ants possess so discriminating a sense of smell, and are so exacting concerning an adherence to the criterion established for their nest, and since even those ants who have had an extended experience in ant-odors, and who have been queenless for two years, refuse to affiliate with a queen of an alien odor though of their own variety, we may hardly expect that they will voluntarily associate with queens of another species. During the summer of 1905 I introduced queens of other species into segregated, queenless groups of adult *Stenamma fulvum*, of *Formica neogates* and of *Formica schaufussi*, that had had their sense of smell highly educated by long association with workers of two or three different species of ants, but in every case the introduced queen was killed within a few days, in spite of her constant efforts to keep aloof from the workers.

In no species of ant have I found workers that would tolerate the presence of any queen of unfamiliar odor, nor any queen that would willingly remain among workers of unfamiliar odor. Although all species of ants have not been thus tested we may well assume that what is shown to be a fundamental trait in a few species will manifest itself in all species of the tribe.

## V. EFFECTS OF THE PROGRESSIVE ODOR IN THE COMMUNAL LIFE OF ANTS.

Since the queen is ordinarily the earliest occupant of the ant-nest, and since her callow young have the same odor as herself, the odor of her earliest nest must at first be the same as is that of the queen. Probably this odor is at all times dominant in the permanent nest; but as the progressive odor of the workers is gradually added thereto, the nest-aura would be thereby modified. The change in the nest-aura, cumulative with the age of the colony and the increase of the inmates, would be so gradual that all habitants of the nest would at all times find it familiar and therefore congenial. The greater dominance of the queen's odor in the earlier nest may be the cause of the persistence with which many workers cling or return to the old habitation even after the majority of the colony has for sound reason removed to a new abode.

It appears probable also that diffused ant-odor is in direct ratio to bulk of ant-body, and that a cause of the common activity of workers in adding the lesser to the larger pile of brood, sometimes even against the inhibitory effects of light, is due to the more manifest odor of the larger pile.

I have at different times during several years observed in my artificial nests a most curious phenomenon among ants that had long lived amicably together. Several or many workers were seen standing around one ant as if holding a court of inquiry concerning this associate. Sometimes the associate is proscribed, sometimes rent limb from limb. This extraordinary behavior is probably due to the victim having attained a progressive odor that is obnoxious to many other inmates of the nest because unknown to them. This might happen to an aged ant whose horde of companions were all young. It might also happen that in prowling for food, or in raids made on the nests of aliens, the worker ants would bring in alien young for food, and that this much licked and tended young would incur the progressive odor of the nurses. At a later period the introduced ant might produce a progressive odor unlike that of the multitude inhabiting the nest, and it would therefore be doomed to destruction. Ostracisms or violent

deaths, such as sometimes occur in nests where amity has long prevailed, are probably to be explained by the attainment by some of the inmates of a new and therefore an alarming progressive odor.

There may be seen among ants of the same variety, and even in the same individual, all degrees of attraction and repulsion towards other ants at a first meeting with them. Such manifestations range all the way from cuddling, caressing, cherishing devotion through indifference and inattention, distrust, suspicion, animosity and enduring, ferocious enmity. The inciting cause is doubtless the progressive odor of the visitor, and the practical end is the preservation of the chemical standard of the nest.

Whatever the action of the ants, it is always more obvious when there are numerous young in the nests, and when the nest-aura is well established.

During five years of fairly constant study of ants I have seen no evidence that their antennæ are the organs of any other sense than the chemical sense, and I am convinced that any statement concerning the behavior of ants may well be distrusted if it ignore the dominance of the olfactory sense over the conduct of the ant, the ant's almost inconceivable minuteness of discrimination in odors, or the ant's marvelous memory of odors that have been encountered. Only when ants are segregated from the pupa-stage, and full record kept of every experience of theirs in meeting other ants, can the investigator truthfully declare that ants behave in a certain manner in the presence of other ants. Moreover, as every ant acts on personal experience and individual memory, the ants should be considered singly as well as in groups and communities, when a theory of their behavior is to be enunciated. But when the total history of an ant is known, the investigator may accurately predict the behavior of that ant toward other ants. There is exceeding uniformity of behavior among ants having an identical history.

The progressive odor of the worker ants is manifestly an advantage in their communal life, since it furnishes the means whereby every ant can recognize its home and its fellow-citizens, avoiding nests and communities other than its own. The uses of this odor within the colony may also be numerous, and it may determine the distribution of labor in the ant community.



Through the male element, it probably differentiates the odor of queens of the same species, enabling the workers to find, to defend, and to cherish their own queen.

It differentiates ants otherwise alike ; determines their distribution in separate communities ; dictates the behavior of members of one colony toward those of another colony, and in connection with an acute sense of smell and a powerful memory, is a dominant factor in the life of the individual ant and in the structure of the ant-colony.